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Global diversity and distribution of arbuscular mycorrhizal fungi

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ABSTRACT

Arbuscular mycorrhizal (AM) fungi form associations with most land plants and can control carbon, nitrogen, and phosphorus cycling between above- and belowground components of ecosystems. Current estimates of AM fungal distributions are mainly inferred from the individual distributions of plant biomes, and climatic factors. However, dispersal limitation, local environmental conditions, and interactions among AM fungal taxa may also determine local diversity and global distributions. We assessed the relative importance of these potential controls by collecting 14,961 DNA sequences from 111 published studies and testing for relationships between AM fungal community composition and geography, environment, and plant biomes. Our results indicated that the global species richness of AM fungi was up to six times higher than previously estimated, largely owing to high beta diversity among sampling sites. Geographic distance, soil temperature and moisture, and plant community type were each significantly related to AM fungal community structure, but explained only a small amount of the observed variance. AM fungal species also tended to be phylogenetically clustered within sites, further suggesting that habitat filtering or dispersal limitation is a driver of AM fungal community assembly. Therefore, predicted shifts in climate and plant species distributions under global change may alter AM fungal communities.

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1. Introduction

The relative importance of dispersal limitation, environmental filtering, biotic interactions, and neutral processes for structuring biological communities remains unresolved for many organisms (Hubbell, 2001; Leibold et al., 2004). Moreover, although much work has documented spatial, environmental, and biological mechanisms that limit the distributions of plants and animals (Lomolino et al., 2005), the roles of these factors in microbial biogeography are less clear (Martiny et al., 2006). Some microorganisms exhibit species-area relationships and co-occurrence patterns that are equivalent to those of macroorganisms (Horner-Devine et al., 2004; Horner-Devine et al., 2007; Peay et al., 2007), while other microbial taxa have more cosmopolitan distributions (Fenchel and Finlay, 2005; Finlay, 2002). In particular, the biogeography of mycorrhizal fungi remains relatively unknown at the global scale despite recent advances in understanding global distributions of other microorganisms (Horner-Devine et al., 2004; Martiny et al., 2006).

Arbuscular mycorrhizal (AM) fungi colonize ~75% of plant species (Newman and Reddell, 1987) and provide numerous benefits to their hosts, including increased N and P acquisition, drought tolerance, and pathogen protection (Auge, 2001; Johnson et al., 2010; Sikes et al., 2009). In these associations, AM fungi receive up to 30% of the host's photosynthate (Drigo et al., 2010). In addition, AM fungal taxa can differ in their influences on net primary productivity (NPP), plant competition, aboveground plant diversity, and higher trophic levels (Mack and Rudgers, 2008; Maherali and Klironomos, 2007; Pearson and Jakobsen, 1993; Sikes et al., 2009; Sikes et al., 2010; van der Heijden et al., 2008; van der Heijden et al., 1998).

Given that AM fungi are best known for their relationships with plants, it is perhaps not surprising that current AM fungal biogeography is primarily defined by the global distribution of known plant hosts and plant-defined biomes (Allen et al., 1995; Öpik et al., 2010). For instance, AM fungal communities are expected to dominate grasslands, but not boreal forests (Allen et al., 1995; Read, 1991). Indeed, the biomass and community composition of AM fungi differ with respect to biome, invasive plants, and plant species richness (Hawkes et al., 2006; Helgason et al., 2002; Kivlin and Hawkes, 2011; Öpik et al., 2006; Treseder and Cross, 2006), supporting the idea that spatial variation in plant community structure at many scales influences the distribution of AM fungal taxa.

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Dispersal limitation, environmental filtering, and biotic interactions between AM fungal taxa, however, may also contribute to their biogeography (Dumbrell et al., 2010; Lekberg et al., 2007). Arbuscular mycorrhizal fungi produce relatively large spores (up to ~640 µm) that are mainly wind or animal dispersed over intermediate ranges (<2 km); their hyphae can be dispersed over smaller areas (<10 m) (Mangan and Adler, 2000; Warner et al., 1987). Both can restrict the range of AM species. Nevertheless, the recent human-mediated introduction of microorganisms in soil and plant inoculum could result in large-scale dispersal of AM fungi (Schwartz et al., 2006; Vellinga et al., 2009). Distributions of arbuscular mycorrhizal fungi are also affected by many environmental parameters. For example, soil type and texture, disturbance, moisture, temperature, and nutrient availability are often correlated with AM fungal composition (Hawkes et al., 2011; Lekberg et al., 2007; Pringle and Bever, 2002; Rillig et al., 2002).

Trade-offs in phylogenetically-conserved traits have occurred during the evolution of the Glomeromycota lineage, affecting the growth of the fungus and plant host (Hart and Reader, 2002; Koide, 2000; Maherali and Kironomos, 2007; Powell et al., 2009). For example, Hart and Reader (2002) demonstrated that members of the Gigasporaceae family preferentially produce extraradical hyphal biomass in the soil, while members of the Glomeraceae family extensively colonize roots. These trade-offs in hyphal traits contribute to higher nutrient acquisition and biomass of plants in symbiosis with Gigasporaceae species, and greater pathogen protection of plants that associate with Glomeraceae species (Powell et al., 2009). They are also hypothesized to affect AM distributions; Glomeraceae species are expected to be prevalent in high nutrient soils while Gigasporaceae are predicted to dominate in low nutrient conditions (Treseder, 2005). These long-existing trade-offs may also lead to interactions between AM fungal taxa that could affect community assembly. If traits are phylogenetically conserved, competitive exclusion between closely related AM fungi could lead to a community in which species are less related than expected by chance (i.e., phylogenetic overdispersion). Alternatively, if environmental filtering or dispersal limitation selects for these traits, species within AM fungal communities could be more closely related than expected by chance (i.e., phylogenetic clustering) (Webb et al., 2002).

Arbuscular mycorrhizal fungi are often considered generalists, since only 200–300 species have been described to date (Öpik et al., 2010; Schüßler and Walker, 2010). However, current estimates of AM fungal diversity are largely based on spore morphology (Morton, 1988), which does not always separate genetically distinct taxa (Hijri and Sanders, 2005). Molecular surveys of AM fungi at the regional scale or larger are uncommon and have thus far been restricted to only one gene (18S) in the most abundant taxa (Dumbrell et al., 2010; Öpik et al., 2006, 2010). For example, Öpik et al. (2010), discovered that the distributions of the majority of AM fungal taxa are affected by associations with broad plant lineages or climate zones (i.e., tropical vs. temperate regions), but were unaffected by latitude, elevation or plant species richness. Here we expand upon these approaches by comparing the relative influence of spatial, environmental, and biotic drivers on global AM fungal distributions and examining how these factors, along with phylogenetic trait conservation, can structure local AM fungal communities. To our knowledge, our study is the first to examine how AM fungal community composition relates to soil characteristics and phylogenetic history on the global scale. We independently confirmed our analyses by comparing two genetic loci; the 18S and 28S genes.

We conducted a synthesis of published DNA sequences to determine controls over AM fungal distributions and community composition on the global scale. We hypothesized that AM fungi

would be dispersal limited, owing to large spore size and below-ground spore production. In addition, we predicted that AM fungal community composition would vary as a function of climate, soil characteristics, and plant community type. We predicted that local AM fungal communities would be phylogenetically clustered if environmental selection or dispersal limitation controlled community assembly, or overdispersed if interactions between fungal taxa were prevalent. We hypothesized that if AM fungi were influenced by one or more of these filters, community composition would differ significantly between sites (i.e., exhibit high beta diversity), perhaps leading to higher global diversity than previously estimated. Our analysis differs from other recent approaches in that we focus on how community-level interactions (based on phylogenetic history) affect AM fungal distributions and compare the relative strengths of abiotic, biotic and spatial drivers affecting community assembly patterns.

2. Materials and methods

2.1. Sequence collection

Fungal 18S and 28S sequences were compiled from GenBank using the search terms of “soil, grassland, litter, tundra, agriculture, marsh, permafrost, forest, or desert” and “fung*”. All sequences were downloaded by 03/15/2010. We only included sequences collected from natural habitats that had not been manipulated by fertilization, tillage or heavy metal disturbances. We collected 9905 18S and 5056 28S Glomeromycota sequences from both published and unpublished sources. All non-identical sequences were used to determine diversity metrics. For all other community analyses, we focused on studies that reported 16 or more sequences and 3 or more operational taxonomic units (Tables S1 and S2), resulting in the inclusion of 4680 18S sequences and 1896 28S sequences from 72 studies for the 18S region and 39 for the 28S region (see Fig. S1 for distribution of study sites). This approach allowed us to sample depauperate communities, but also ensured that sampling depth was adequate to capture additional diversity if it existed in the community. The number of sequences reported (i.e., sampling intensity) was not significantly correlated to the number of operational taxonomic units (OTUs, i.e., taxa defined by genetic identity) described for each study ($r^2 = 0.019$). This lack of a trend was largely driven by datasets containing few OTUs but many sequences, even though the smallest datasets tended to contain fewer OTUs. In general, there were many singleton OTUs: up to 54% for the 18S gene dataset. Nevertheless, the community-level trends were robust when analyzed with singletons and low sampling intensity sites excluded, indicating that sampling intensity and singleton distributions were not main explanatory variables in our dataset (but see Unterseher et al., 2011).

All Glomeromycota species were assumed to form AM fungal associations, and all studies were assumed to include bulk soil and root fragments. While this may not always have been the case, sampling methods were not available for unpublished studies and therefore could not be assessed. To compare sites, we limited the 18S sequences to a 500-bp region between the NS31 and AM1 primers, while the 28S sequences were from a 500-bp region in the D1/D2 variable region. We analyzed both gene regions, as the 18S conserved region captures distant evolutionary events (i.e., dispersal limitation over paleological time periods), while the 28S variable region represents more recent evolutionary adaptations (i.e., local environmental specialization). Furthermore, by comparing these gene regions, we can avoid the sampling biases inherent in the distribution of study locations, and determine if gene-specific evolution rates hinder comparison between studies conducted on different gene regions.

2.2. Phylogenies

Sequences were aligned separately for each gene to an existing internal guide tree of over 200 known Glomeromycota sequences using SATé (Liu et al., 2009). We also used SATé to estimate phylogenies using the default parameters of 100 iterations under the Gamma GTR substitution model (Figs. S2 and S3 for 18S and 28S trees respectively). SATé was employed in this study as it has consistently produced more accurate alignments and phylogenies for gene sequences that are variable (such as 28S sequences) (Liu et al., 2009). Guide tree sequences were compiled from known databases, and only unknown sequences that were within known clades were retained for our analyses (Pruesse et al., 2007; Stockinger et al., 2010). We further confirmed that our sequences were Glomeromycota by performing a BLAST search utilizing the BLASTN algorithm with an expect value of 10^{-6} in the GenBank database (Altschul et al., 1990). To define OTU groups, we collapsed monophyletic taxa at the 97% and 99% sequence similarity levels. We analyzed the data at different OTU similarity levels, as the OTU designation has been shown to affect biogeographic patterns in other systems (e.g., Martiny et al., 2009). We analyzed OTUs at the 97% and 99% similarities, as these designations are widely employed for AM fungal communities (Haug et al., 2010; Öpik et al., 2010). Our OTU designations differ, however, from most estimates of AM fungal diversity in that our OTUs are based on both sequence similarity and shared phylogenetic history; most estimates to date are exclusively based on the former (Bever et al., 2001; Husband et al., 2002; Lekberg et al., 2007; but see Öpik et al., 2010). Our method is more stringent than OTU-calling based on sequence similarity alone, but the two methods consistently provide similar richness estimates (Kivlin and Hawkes, 2011) and are comparable with newer, evolutionary approaches (Powell et al., 2011).

2.3. Environmental data

All designations of plant communities and geographic locations were obtained from the primary literature. Other environmental variables were taken from the primary literature where available. Otherwise, elevation was collected from Google Earth. Mean annual precipitation and temperature, NPP, soil series, pH, soil moisture, soil temperature, soil organic C concentration, potential evapotranspiration (PET), and relative humidity were collected from Atlas of the Biosphere (Foley et al., 1996; Kucharik et al., 2000; New et al., 1999). Designations of soil moisture and temperature follow the USDA-NRCS taxonomy, which uses quantitative, temporal and soil texture parameters to determine soil microclimate (Soil Survey Staff, 2010). Only variables that did not correlate over 40% with other variables were retained for subsequent analyses; this similarity cutoff only excluded evapotranspiration, which was strongly correlated to the included variable of potential evapotranspiration (PET).

2.4. Data analysis

Diversity estimates were calculated as the total number of monophyletic OTUs observed at the 97% and 99% similarity cutoffs for each gene region. To understand if the global diversity estimates obtained in this study were linked to beta diversity between sites versus alpha diversity within sites, we also determined the total number of sites in which each taxon was observed. Alpha diversity was defined as the number of AM fungal taxa present at a single site. Beta diversity was calculated as the total number of AM fungal taxa (gamma diversity)/the average alpha diversity per site (Whittaker, 1972). All diversity metrics are presented with ± 1 standard error. Separately, we used the Chao1 diversity index to

determine the potential global diversity of AM fungi (EstimateS v. 8.2, Colwell, 2009).

To examine the relative importance of potential spatial, environmental, and biotic controls over AM fungal OTU distributions, we used non-parametric PerMANOVA to simultaneously analyze spatial (latitude, longitude and elevation), climatic (temperature, precipitation, humidity, PET), soil (soil series, soil moisture, soil temperature, pH), and plant (composition and NPP) variables (R Development Core Team, 2009). Because this method is sensitive to the order of analyses, we randomized the order of analysis for all variables and only retained those that were significant in all 999 runs. In addition, we tested for specific differences in fungal community composition among continents, paleocontinents, plant communities, soil temperature, and soil moisture using multiple response permutation procedures (MRPP) with Bray–Curtis dissimilarity matrices (Mielke and Berry, 2007). These differences were visualized with non-metric multi-dimensional scaling (NMS) (McCune and Mefford, 2006). Where appropriate, *P* values were adjusted for multiple comparisons with the Dunn–Sidak correction factor (Ury, 1976). We present MRPP and PerMANOVA results from the 97% OTU cutoff, as the trends did not differ based on the OTU resolution.

We further examined spatial effects by examining how geographic distance between sites influenced AM fungal community composition. Mantel tests were used to analyze correlations between matrices for geographic distance and the Euclidian distance of community composition, with distances calculated between all possible pairs of study sites for the 18S gene region (Vegan v. 1.15-4, Oksanen et al., 2009). Mantel tests were calculated at the global scale and for North America and Europe, the two most sampled continents. While the Euclidian distance metric equally weighs presence and absence in the community, because our distributions were highly localized (i.e., many more 0s than 1s), other methods such as Bray–Curtis dissimilarities were not appropriate (Clarke et al., 2006).

To further distinguish between spatial, environmental and biotic controllers of local AM fungal community structure, we performed phylogenetic dispersion tests for each study site. We assessed the phylogenetic signal at the tips of the phylogeny using the standardized effect size of the mean nearest taxon distance metric (MNTD), and at the base of the phylogeny using the standardized effect size of the mean phylogenetic distance metric (MPD). All analyses were performed in Picante v. 0.7-2 (Kembel et al., 2010). As conservation of traits is assumed within AM fungal phylogenies (Maherali and Klironomos, 2007), we were able to assess the relative strength of biotic vs. abiotic filters on AM fungal communities over contemporary (MNTD) and evolutionary (MPD) time-scales. Phylogenetic clustering is positively correlated to the geographic area sampled for other organisms (Swenson et al., 2006), so we tested this assumption for our dataset. We observed no difference in phylogenetic signal based on the spatial scale of the species pool. Thus, we assumed a global species pool for our analyses.

3. Results

3.1. AM fungal richness

AM fungal richness was high in our dataset, with 563 OTUs and 669 OTUs observed for the 18S and 28S datasets, respectively, at the 97% similarity cutoff. At the 99% similarity cutoff, we observed 967 OTUs in the 18S region and 1159 OTUs in the 28S region. At the 97% similarity cutoff, the average OTU richness at each site (alpha diversity) was 15.39 (± 1.30) OTUs for 18S and 21.40 (± 3.29) OTUs for 28S. At the 99% similarity cutoff, alpha diversity increased

marginally to 17.57 (± 1.51) OTUs for the 18S sequences and 30.27 (± 4.93) OTUs for the 28S sequences. There was little overlap between AM fungal communities at different sites. For example, from the 18S dataset at the 97% OTU cutoff, 379 OTUs were found at single sites, while the most cosmopolitan taxon was found only at 18 of the 71 sites (Fig. 1a). This pattern was similar for the 18S sequences at the 99% OTU cutoff and the 28S region (Fig. 1b, c, d). This variation led to high beta diversity estimates ranging from 36.58 and 31.26 for 18S and 28S regions at the 97% cutoff to 55.04 and 38.29 for 18S and 28S regions at the 99% cutoff. These estimates of diversity were further supported by high Chao1 estimates of overall fungal diversity: ranging from 789 and 1321 OTUs for the 18S and 28S regions at the 97% cutoff to 1442 and 2636 OTUs at the 99% cutoff for the 18S and 28S regions respectively.

3.2. Community composition: spatial effects

Spatial factors were significant drivers of AM fungal distributions, with significant clustering by continent for the 18S ($T = -7.138$, $A = 0.021$, $P < 0.001$) and 28S datasets ($T = -7.439$, $A = 0.045$, $P < 0.001$). In the 18S dataset, AM fungal communities were distinct among all continents except Australia, which had the most variability in AM fungal communities and thus did not differ from South America ($T = -0.429$, $A = 0.008$, $P = 0.260$), Europe ($T = -0.751$, $A = 0.003$, $P = 0.177$), Asia ($T = -0.518$, $A = 0.009$, $P = 0.184$) or North America ($T = 0.042$, $A = -0.003$, $P = 0.230$). The 28S dataset was consistent with the 18S results, but statistically different AM fungal communities only occurred between Europe and South America ($T = -0.251$, $A = 0.050$, $P < 0.001$) (Fig. 2). Clustering by paleocontinent was evident in the 18S dataset, with continents of former Laurasia (North America, Europe and Asia) grouping distinctly from those found in former Gondwanaland (South America, Australia and Africa) ($T = -5.493$, $A = 0.006$, $P < 0.001$). At the global scale, AM fungal communities also became more dissimilar as the geographic distance between the sites

increased, albeit with a high degree of unexplained variation ($r^2 = 0.035$, $P < 0.001$) (Fig. 3). Within continents, however, AM fungal communities did not differ significantly with geographic distance (Europe $r^2 = 0.0196$, $P = 0.188$, North America $r^2 = 0.026$, $P = 0.22$).

3.3. Community composition: habitat effects

Plant biomes appeared to influence AM fungal community composition, with distinct fungal communities found across the dominant habitats. In the 18S dataset, all plant biomes examined (agriculture, grasslands, forests and wetlands) contained distinct AM fungal communities (Fig. 4; $T = -4.626$, $A = 0.009$, $P < 0.001$), while in the 28S dataset only grasslands were distinct from agriculture ($T = -2.740$, $A = 0.011$, $P = 0.014$) and wetlands ($T = -2.520$, $A = 0.010$, $P = 0.020$). The community composition of AM fungi was only marginally affected by plant NPP in the 18S dataset at the 97% cutoff ($r^2 = 0.017$, $P = 0.010$).

3.4. Community composition: abiotic effects

Environmental factors also co-varied with AM fungal distributions, with the strongest relationships observed for soil temperature (18S: $T = -8.060$, $A = 0.020$, $P < 0.001$; 28S: $T = -3.267$, $A = 0.020$, $P = 0.010$) and soil moisture (18S: $T = -6.070$, $A = 0.0145$, $P < 0.001$; 28S: $T = -1.299$, $A = 0.008$, $P = 0.105$) (Fig. 5). Relative humidity, PET, soil pH, and soil series also affected distributions based on PerMANOVA, but to a lesser extent (Table 1).

The relative contributions of spatial (latitude, longitude, and continent), plant community, and other environmental factors affecting AM fungal distributions were similar based on the results of the PerMANOVA model. Each variable explained a small, but significant, portion of the variance (1.18–4.47%) in AM fungal community composition between sites (Table 1). Furthermore, we found significant interactions between geographic, plant

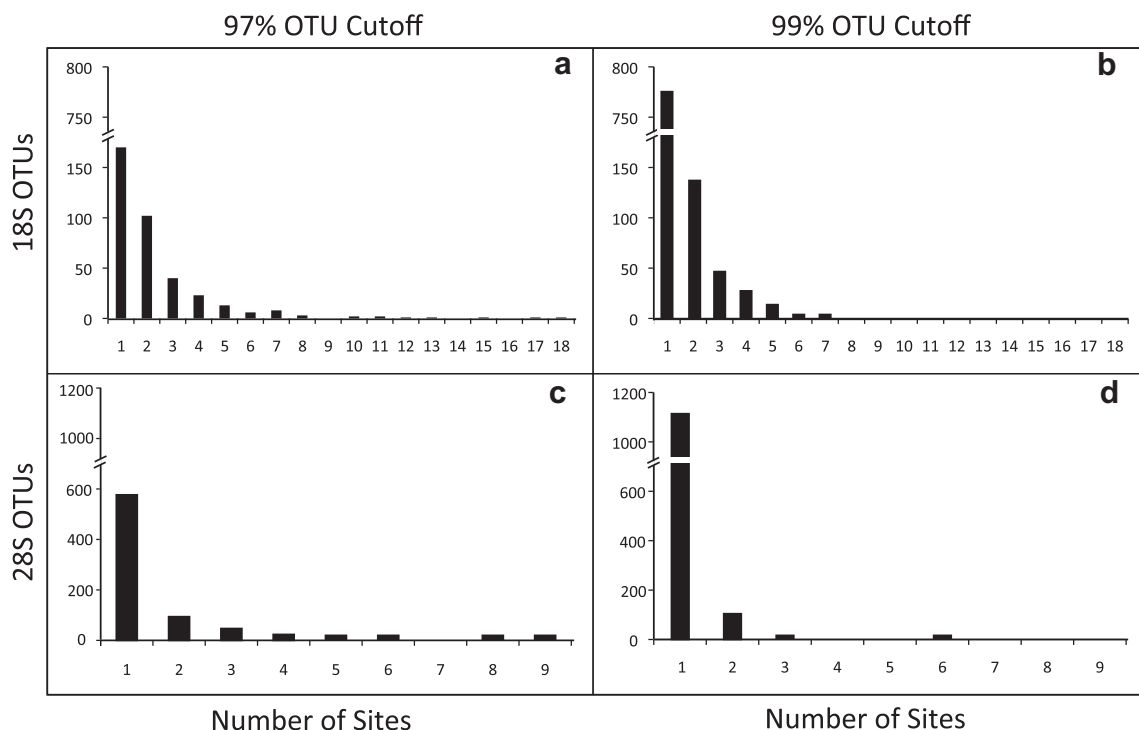


Fig. 1. Distribution of OTUs for the 18S and 28S datasets at the 97% and 99% similarity cutoffs. The number of sites that each OTU occurs in is on the X axis. Most OTUs only occur at one site. As the OTU similarity cutoff is increased, the overlap between sites is diminished.

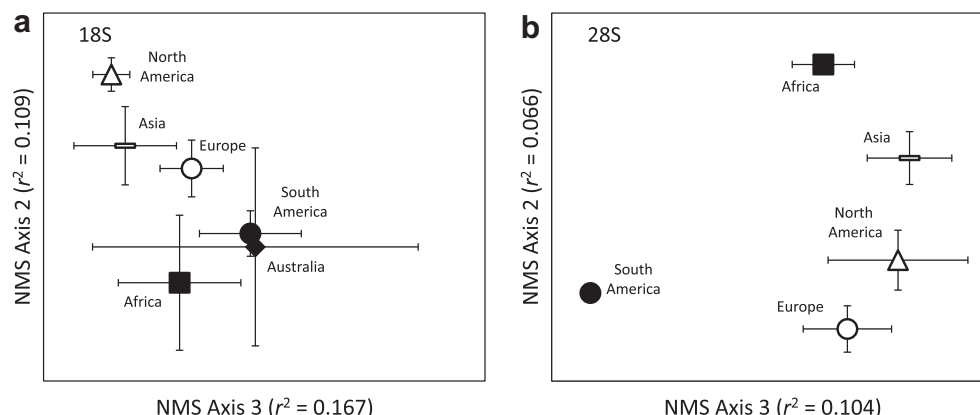


Fig. 2. Nonmetric Multidimensional Scaling (NMS) of AM fungal communities by continent for (a) the 18S dataset and (b) 28S dataset based on the 97% OTU designation. Open symbols correspond to continents formerly in Laurasia and closed symbols correspond to continents formerly in Gondwanaland. Mean (± 1 SE) NMS estimates are plotted. Final stress values after 500 iterations were (a) 25.8472 and (b) 26.107.

community, and environmental factors, indicating that plant community and environmental mechanisms may have differed in their effects on AM fungal community composition depending on geographic location. Plant communities are known to co-vary with climatic variables, though, which may have affected our results (Table 1).

3.5. Community-level phylogenetic effects

Phylogenetic dispersion patterns revealed a trend of phylogenetic clustering for terminal and basal nodes in over 50% of sites for both the 18S and 28S datasets at the 97% and 99% sequence similarity cutoffs (Table S2). This trend was consistently more prevalent in the MNTD metric, indicating the potential for relatively recent genetic convergence at the community level. Moreover, MNTD and MPD values were typically more clustered for 28S communities relative to 18S communities, providing some evidence for more rapid evolution in the 28S gene. Conversely, phylogenetic over-dispersion was only observed in two sites out of 111.

4. Discussion

Arbuscular mycorrhizal fungal diversity in our study was higher than previously observed in morphological and molecular surveys: up to three times higher at the 97% similarity level and six times higher at the 99% similarity level (Öpik et al., 2010; Schüssler and Walker, 2010). However, these high estimates were not due to high species richness within study sites; alphadiversity within sites was typically less than 25 OTUs. Instead, taxa were site-specific, leading to high beta diversity between sites. Indeed, phylogenetic clustering of closely related taxa was common at the majority of our sites, suggesting that radiation of AM fungal lineages within local sites may be prevalent. High beta diversity has recently been highlighted in other studies of global AM fungal distributions, which indicated that up to 33% of AM fungal taxa occurred in single biogeographical provinces (Dumbrell et al., 2010; Öpik et al., 2010). Certainly, lower similarity definitions for AM fungal taxa (e.g., 80% in Allison and Treseder, 2008) would result in lower estimates of diversity. Our OTU cutoffs are typical of species to genus level definitions of fungal taxa and are consistent with the majority of current work on AM fungal sequences (Dumbrell et al., 2010; Haug et al., 2010; Öpik et al., 2010). Furthermore, these OTU designations have been demonstrated to coincide with alternative species richness estimates based on evolutionary criteria (Powell et al., 2011). Moreover, our diversity estimates based on the Chao1 index point to the possibly of many undiscovered AM fungal taxa—up to four times more than those described in the present study. In addition, numerous other studies have demonstrated that current sampling efforts for AM fungi are not extensive enough to capture total species richness (Helgason et al., 2002; Husband et al., 2002; Lekberg et al., 2007; Öpik et al., 2010). Arbuscular mycorrhizal fungi are known to contain multiple genomes within single spores as well as genetic variation within morpho-species (Hijri and Sanders, 2005; Morton, 1988; Stockinger et al., 2009), which may have contributed to greater molecular-based diversity than morphological-based diversity.

High beta diversity between sites can result from multiple mechanisms, which need not be mutually exclusive. For example, a combination of dispersal limitation, plant host effects, and variation in other environmental conditions such as soil temperature and moisture could result in the large compositional variation we observed between sites. High rates of spatial variation in AM fungal taxa have been observed in many habitats, including within a 100-ha old field, within isolated patches of tropical and temperate

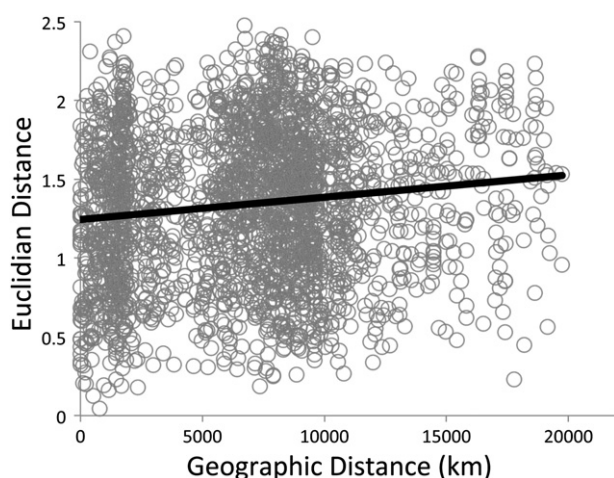


Fig. 3. Mean Euclidian distance of community composition in the 18S dataset at the 97% cutoff is plotted against the geographic distance between sites in kilometers. Mean Euclidian distance between sites was positively correlated to geographic distance between sites ($r^2=0.035$). Although, similar communities still occur over vast distances and geographically close sites sometimes contain dissimilar communities.

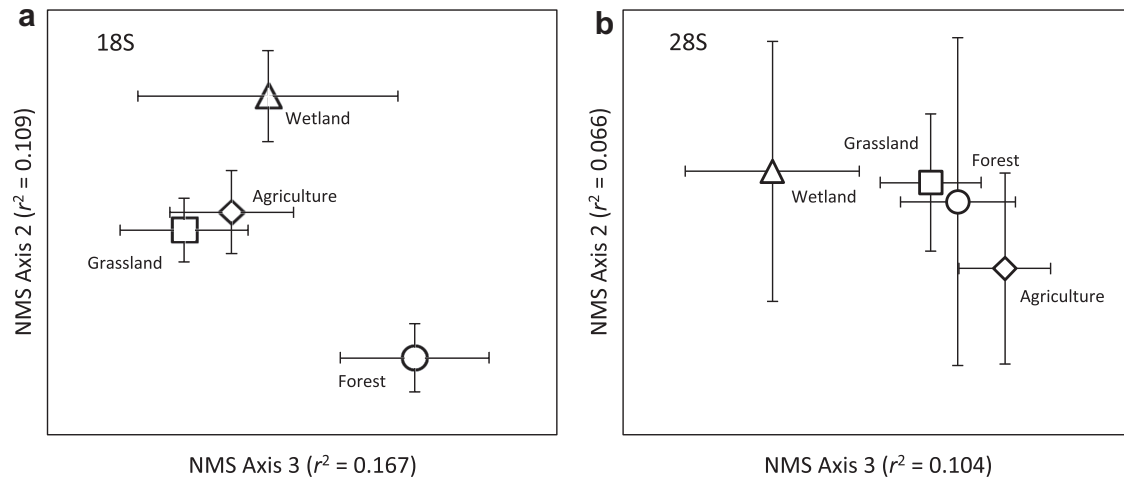


Fig. 4. Nonmetric Multidimensional Scaling (NMS) of AM fungal communities by plant community for (a) the 18S dataset and (b) 28S dataset based on the 97% OTU designation. Mean (\pm SE) NMS estimates are plotted. Final stress values after 500 iterations were (a) 25.8472 and (b) 26.107.

forests, and across African grasslands (Bever et al., 2001; Lekberg et al., 2007; Mangan et al., 2004; Peay et al., 2007). However, a mechanistic understanding of this spatial variation is lacking, especially at the global scale.

One scenario is that AM fungi possess more specialized host plant associations than previously recognized. Although AM fungi are thought to be predominantly generalists, certain AM fungal taxa

have been shown to be more host specific than others (Helgason et al., 2002; Husband et al., 2002; Öpik et al., 2009; Smith and Read, 2008). Associations between AM fungi and host plant species can vary spatially, even over small distances, which could further explain the high variation in AM fungal community composition between our study sites (Klironomos, 2003). While our analysis could not determine levels of host specificity, the

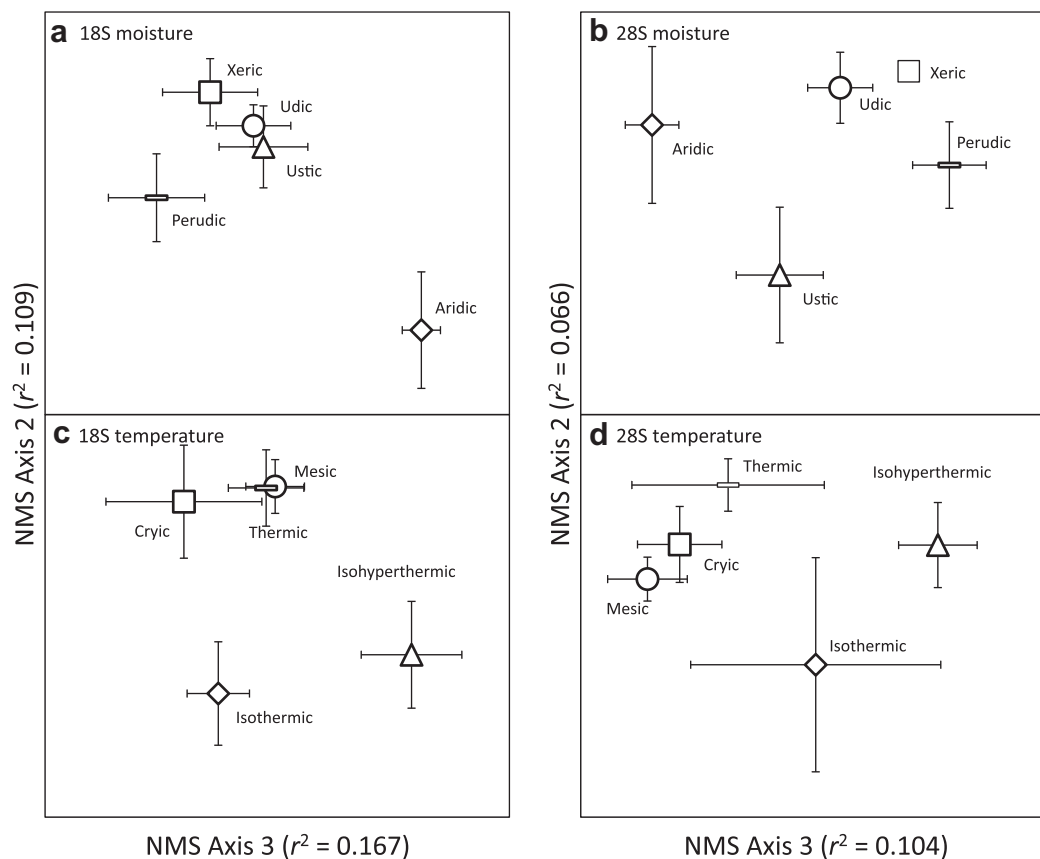


Fig. 5. Nonmetric Multidimensional Scaling (NMS) of AM fungal communities by soil moisture (a, b) and temperature (c, d) for the 18S dataset (a, c) and the 28S dataset (b, d) based on the 97% OTU designation. Soil moisture and temperature designations follow USDA-NRCS taxonomy. Briefly, soil moisture from driest to wettest is Aridic, Xeric, Ustic, Udic, Perudic, while soil temperature from coldest to warmest is Cryic, Mesic, Thermic, Isothermic, Isohyperthermic. Mean (\pm SE) NMS estimates are plotted. Final stress values after 500 iterations were (a) 25.8472 and (b) 26.107.

Table 1

PerMANOVA values for the 18S and 28S datasets at the 97% sequence similarity run after 999 iterations. Boldface type indicates $P < 0.05$.

	Df	Sum of squares	Mean sum of squares	F. Model	r^2	P
18S 97% PerMANOVA results						
Latitude	1	0.979	0.979	3.309	0.030	0.01
Longitude	1	0.617	0.617	2.086	0.019	0.01
Elevation	1	0.553	0.553	1.870	0.017	0.01
Plant	1	0.561	0.561	1.897	0.017	0.01
Precipitation	1	0.564	0.564	1.906	0.017	0.01
Temperature	1	0.677	0.677	2.288	0.021	0.01
Humidity	1	0.673	0.673	2.275	0.021	0.01
PET	1	0.714	0.714	2.411	0.022	0.01
pH	1	0.685	0.685	2.315	0.021	0.01
Soil series	1	0.440	0.440	1.487	0.013	0.01
NPP	1	0.552	0.552	1.867	0.017	0.01
Organic matter	1	0.447	0.447	1.512	0.014	0.01
Soil moisture	1	0.699	0.689	2.328	0.021	0.01
Soil temperature	1	0.418	0.418	1.413	0.013	0.01
Latitude:Longitude	1	0.440	0.440	1.487	0.013	0.01
Latitude:Elevation	1	0.553	0.553	1.867	0.017	0.01
Longitude:Elevation	1	0.479	0.479	1.617	0.015	0.01
Latitude:Plant	1	0.609	0.609	2.059	0.019	0.01
Longitude:Plant	1	0.609	0.609	2.056	0.019	0.01
Elevation:Plant	1	0.453	0.453	1.529	0.014	0.01
Latitude:Precipitation	1	0.435	0.435	1.469	0.013	0.02
Longitude:Precipitation	1	0.625	0.625	2.113	0.019	0.01
Elevation:Precipitation	1	0.378	0.378	1.276	0.012	0.08
Plant:Precipitation	1	0.620	0.620	2.095	0.019	0.01
Latitude:Temperature	1	0.486	0.486	1.641	0.015	0.01
Longitude:Temperature	1	0.537	0.537	1.813	0.016	0.01
Elevation:Temperature	1	0.430	0.431	1.454	0.013	0.02
Plant:Temperature	1	0.431	0.431	1.456	0.013	0.01
Precipitation:Temperature	1	0.456	0.456	1.539	0.014	0.01
Latitude:Humidity	1	0.487	0.487	1.645	0.015	0.01
Longitude:Humidity	1	0.503	0.503	1.699	0.015	0.01
Elevation:Humidity	1	0.485	0.485	1.640	0.015	0.01
Plant:Humidity	1	0.384	0.384	1.296	0.012	0.03
Precipitation:Humidity	1	0.476	0.476	1.609	0.015	0.01
Temperature:Humidity	1	0.497	0.497	1.678	0.015	0.01
Latitude:PET	1	0.444	0.444	1.501	0.014	0.01
Longitude:PET	1	0.437	0.437	1.475	0.013	0.01
Elevation:PET	1	0.440	0.440	1.485	0.013	0.01
Plant:PET	1	0.351	0.351	1.186	0.011	0.1
Precipitation:PET	1	0.381	0.381	1.289	0.012	0.02
Temperature:PET	1	0.469	0.469	1.584	0.014	0.01
Humidity:PET	1	0.475	0.475	1.605	0.015	0.01
Latitude:pH	1	0.403	0.403	1.362	0.012	0.03
Longitude:pH	1	0.456	0.456	1.542	0.014	0.01
Elevation:pH	1	0.386	0.386	1.305	0.012	0.03
Plant:pH	1	0.372	0.372	1.255	0.011	0.08
Precipitation:pH	1	0.428	0.428	1.447	0.013	0.01
Temperature:pH	1	0.357	0.357	1.206	0.011	0.07
Humidity:pH	1	0.452	0.452	1.528	0.014	0.01
PET:pH	1	0.445	0.445	1.505	0.014	0.02
Latitude:Soil Series	1	0.690	0.690	2.332	0.021	0.01
Longitude:Soil Series	1	0.386	0.386	1.305	0.011	0.03
Elevation:Soil Series	1	0.370	0.370	1.251	0.011	0.13
Plant:Soil Series	1	0.303	0.303	1.023	0.009	0.32
Precipitation:Soil Series	1	0.431	0.431	1.458	0.013	0.01
Temperature:Soil Series	1	0.422	0.422	1.425	0.013	0.01
Humidity:Soil Series	1	0.442	0.441	1.492	0.013	0.01
PET:Soil Series	1	0.450	0.450	1.519	0.014	0.01
pH:Soil Series	1	0.546	0.546	1.844	0.017	0.01
Latitude:NPP	1	0.490	0.490	1.654	0.015	0.01
Longitude:NPP	1	0.366	0.366	1.238	0.011	0.06
Elevation:NPP	1	0.346	0.346	1.169	0.011	0.03
Residuals	8	2.368	0.296		0.072	
Total	70	32.849			1	
28S 97% PerMANOVA results						
Latitude	1	0.737	0.737	1.646	0.038	0.033
Longitude	1	0.874	0.874	1.951	0.045	0.025
Elevation	1	0.580	0.580	1.294	0.030	0.062
Plant	1	0.581	0.581	1.298	0.030	0.089
Precipitation	1	0.692	0.692	1.545	0.035	0.042

Table 1 (continued)

	Df	Sum of squares	Mean sum of squares	F. Model	r^2	P
Temperature	1	0.575	0.575	1.283	0.029	0.087
PET	1	0.542	0.542	1.210	0.028	0.124
pH	1	0.499	0.499	1.113	0.026	0.192
Soil series	1	0.481	0.481	1.075	0.025	0.291
NPP	1	0.445	0.445	0.993	0.023	0.406
Organic matter	1	0.617	0.617	1.377	0.032	0.076
Soil moisture	1	0.522	0.522	1.166	0.027	0.155
Soil temperature	1	0.496	0.496	1.108	0.025	0.228
Latitude:Longitude	1	0.514	0.514	1.148	0.026	0.181
Latitude:Elevation	1	0.564	0.564	1.258	0.029	0.102
Longitude:Elevation	1	0.442	0.442	0.987	0.023	0.435
Latitude:Plant	1	0.569	0.569	1.271	0.029	0.096
Longitude:Plant	1	0.423	0.423	0.945	0.022	0.560
Elevation:Plant	1	0.499	0.499	1.115	0.026	0.216
Latitude:Precipitation	1	0.450	0.450	1.004	0.023	0.352
Elevation:Precipitation	1	0.513	0.513	1.147	0.026	0.176
Plant:Precipitation	1	0.354	0.354	0.790	0.018	0.909
Latitude:Temperature	1	0.428	0.428	0.956	0.022	0.507
Longitude:Temperature	1	0.430	0.430	0.960	0.022	0.501
Elevation:Temperature	1	0.367	0.367	0.820	0.019	0.840
Plant:Temperature	1	0.463	0.463	1.033	0.024	0.334
Precipitation:Temperature	1	0.309	0.309	0.690	0.016	0.977
Latitude:PET	1	0.422	0.422	0.941	0.022	0.548
Longitude:PET	1	0.499	0.499	1.115	0.026	0.237
Elevation:PET	1	0.416	0.416	0.928	0.021	0.597
Plant:PET	1	0.463	0.463	1.033	0.024	0.330
Precipitation:PET	1	0.382	0.382	0.853	0.020	0.791
Temperature:PET	1	0.372	0.372	0.831	0.019	0.857
Latitude:pH	1	0.320	0.320	0.715	0.016	0.963
Longitude:pH	1	0.468	0.468	1.045	0.024	0.317
Elevation:pH	1	0.442	0.442	0.988	0.023	0.448
Plant:pH	1	0.365	0.365	0.816	0.019	0.867
Precipitation:pH	1	0.412	0.412	0.921	0.021	0.621
Temperature:pH	1	0.120	0.120	0.269	0.006	1
Residuals	7	0.448	0.448		0.023	
Total	48					

differences in AM fungal communities among forest, grassland, agriculture, and wetland plant communities in this synthesis are consistent with some degree of host effects, or factors confounded with host plants. The importance of host effects could occur at a coarse scale, such as trees versus grasses, or could be based on plant host or plant community characteristics such as exotic origin, diversity, priority effects, and neighborhood identity (Hausmann and Hawkes, 2009, 2010; Hawkes et al., 2006; Kivlin and Hawkes, 2011). For example, previous field studies indicate that AM fungal communities are altered by non-native annual grasses in California, with up to an 80% shift in composition between non-native and native plants (Batten et al., 2006, 2008; Hawkes et al., 2006). Recently, Öpik et al. (2010) found that AM fungi with a larger breadth of host plants were also more widely distributed, indicating that the relationship of AM fungi with their plant hosts may play a significant role in AM fungal biogeography.

We also found evidence that local AM fungal communities were affected by dispersal limitation between sites. In addition to the low overlap of taxa among sites, a significant negative relationship between community similarity and distance was observed across sites at the global scale. Distinct clustering in community composition within paleocontinents suggests that long-range dispersal and subsequent establishment of AM fungi over oceans may be relatively uncommon (but see Koske and Gemma, 1990). However, AM fungal communities did not differ significantly within continents, suggesting that dispersal limitation may not be prevalent over shorter spatial scales. Arbuscular mycorrhizal fungal composition did not consistently differ with space; some communities located far apart were more similar than expected and geographical

close sites often differed substantially. Thus, dispersal limitation alone cannot explain trends in AM fungal community composition. Moreover, our ability to detect significant differences in community composition between continents is greatly hindered by the poor sampling in the Southern hemisphere (e.g., Africa = 4 studies, Australia = 2, and South America = 5).

Belowground AM fungal spore production is limited by moisture and nutrient availability (Auge, 2001; Johnson et al., 2003). Thus, spatial and temporal dynamics of spore production as well as wind currents could inhibit dispersal (Warner et al., 1987). Moreover, AM fungal spores are often very large (~40–640 µm) and numerous AM fungal taxa are thought to be largely animal-dispersed, which could lead to a decreased dispersal range compared to mainly wind-dispersed organisms (Mangan and Adler, 2000). All of these factors can reduce the probability that an AM spore will disperse to another ecosystem, reach a suitable location, and colonize a host plant. If dispersal and establishment events are sufficiently low, evolutionary genetic drift in AM fungal taxa within sites could contribute to the high beta diversity we observed in AM species between sites. The prevalent trend of phylogenetic clustering near the tips of both the 18S and 28S phylogenies in the majority of studies examined is consistent with genetic drift (or historical adaptive radiations) playing a role in current AM fungal community assembly.

Environmental factors such as soil moisture and temperature were as important as spatial and plant community variables in their influence on AM fungal communities. Distinct AM fungal taxa were located in warm versus cold sites and in arid versus mesic conditions. Arbuscular mycorrhizal fungi are known to exhibit physiological responses to temperature and moisture, which could affect their environmental tolerance to adverse abiotic conditions (e.g., Hawkes et al., 2008). In laboratory microcosms, freezing and drought have species-specific effects on AM fungal colonization and plant growth with some AM fungal taxa proliferating under drought while others decreased in biomass (Klironomos et al., 2001). Shifts in AM fungal community composition and abundance have also been found in long-term experimental temperature and precipitation manipulations (Hawkes et al., 2011; Rillig et al., 2002). Because basal and terminal nodes within communities were more closely related than expected by chance, environmental filtering may influence community structure.

Because our results are correlative, we cannot confirm whether abiotic controllers and dispersal limitation were the main cause of shifts in AM fungal composition or if these factors, for example, indirectly affected AM fungi via effects on host plant distributions. The effects of spatial autocorrelation in environmental and plant community factors can also result in spatial distance decay relationships in AM community composition, potentially biasing our results (Legendre, 1993). Additionally, many environmental variables co-vary across global scales (e.g., Craine et al., 2009). We excluded variables that co-varied more than 40%, and significant interactions between variables explained less of the variation in composition than single variables alone. Thus, the independent effects of environmental and spatial factors may influence AM fungal communities more than spatial heterogeneity or interactions between abiotic drivers. Our phylogenetic analysis supports the view that spatial and environmental factors structure communities at contemporary and historic timescales. Notably, we observed few examples of phylogenetic overdispersion, indicating that competition between closely related AM fungal taxa does not seem to be structuring AM fungal communities in the systems we examined.

The low predictive power of any of our variables to describe AM fungal distributions suggests that additional factors can affect the structure of AM fungal communities. Arbuscular

mycorrhizal fungi interact with many organisms in the rhizosphere including bacteria, protists and nematodes, all of which are known to affect AM fungal community composition on smaller scales (Fitter and Garbaye, 1994). Local conditions may also play a role, including successional stage, assembly history, and disturbance; these were not captured in our dataset. Other abiotic factors such as nitrogen and phosphorus concentrations, heavy metal contamination, and disturbance history can also influence AM fungal community composition (Hijri et al., 2006; Khan, 2005; Khan et al., 2000; Treseder, 2004). Clearly, multiple factors can influence the distributions of AM fungi, and distinguishing among them at local to global scales will require targeted sampling along environmental and successional gradients over large areas.

5. Conclusions

Overall, we found evidence for substantial differences in AM fungal communities among locations, which resulted in high richness of AM fungal taxa at the global scale. Dispersal limitation, host plant communities, and other environmental factors could contribute to the high variability of AM fungi between sites. Furthermore, environmental filtering and dispersal limitation seemed to influence local AM fungal community assembly patterns.

High turnover between AM fungal communities is of consequence to both restoration efforts and global climate change. The widespread practice of applying AM fungal inoculum to restore plant communities and ecosystem services largely assumes that AM fungal composition does not vary considerably between sites (Schwartz et al., 2006). However, our results indicate that climatic and plant host effects are correlated with AM fungal communities. Therefore, tailoring the origin of AM fungal inocula to match the degraded ecosystem, may improve restoration. In addition, relationships between AM fungal taxa, temperature, and moisture may become particularly germane in the future, as climate change may select for specific AM fungi. If these taxa maintain host-specific interactions with the aboveground plant community or have distinct differences in ecological functions, nutrient dynamics may be altered as a result. These effects could become particularly acute as dispersal limitation could hinder the ability of AM fungal taxa to leave areas that become unsuitable in future climates, leading to local extinction.

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Appendix. Supplementary information

Supplementary information associated with this article can be found in the online version, at doi:10.1016/j.soilbio.2011.07.012.

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